Phenology, Population Dynamics, and Flowering Dynamics of Case's Ladies'-tresses, *Spiranthes casei* var. *casei* (Orchidaceae), in Ottawa, Ontario

JOYCE M. REDDOCH and ALLAN H. REDDOCH

548 Rivershore Crescent, Gloucester, Ontario K1J 7Y7 Canada; e-mail: reddoch@magma.ca

Reddoch, Joyce M., and Allan H. Reddoch. 2008. Phenology, population dynamics, and flowering dynamics of Case's Ladies'-tresses, *Spiranthes casei* var. *casei* (Orchidaceae), in Ottawa, Ontario. Canadian Field-Naturalist 123(1): 19-31.

We describe a seven-year study (2002–2008) of a population of Case's Ladies'-tresses (*Spiranthes casei* var. *casei*) in the western Greenbelt in Ottawa, Ontario, that had been extant since at least 1972. We also record a temporary colonization in the eastern Greenbelt for 11 years (1998–2008). The seven life history stages identified were seed, juvenile, immature, flowering, vegetative, offshoot (ramet), and non-emergent. Mature plants present in the first two years of the study had mean half lives of 9.4 years. Flowering and seed production were limited by damp, cloudy weather when fall rosettes develop, by gastropod herbivory in early summer, by drought in mid-summer, and by deer herbivory in late summer. Given the resulting wide fluctuations in the fractions of plants flowering, as well as the lack of visibility of vegetative plants, this study demonstrates the limitations of annual censuses of flowering stems for determining the actual sizes of populations and for detecting long-term population trends.

Key Words: Case's Ladies'-tresses, *Spiranthes casei*, Brown-lipped Snail, *Cepaea nemoralis*, Banded Wood Snail, *Stethobaris ovata*, White-tailed Deer*, Odocoileus virginianus,* flowering dynamics, gastropod, herbivory, long-term study, population dynamics, Ottawa, Ontario.

Case's Ladies'-tresses (*Spiranthes casei*, pronounced *case-eye*) was described in 1974 by Catling and Cruise (1974). This species is restricted to portions of the Great Lakes – St. Lawrence and Acadian Forest Regions of eastern North America (Rowe 1972; Bailey 1998*). It occurs in parts of Nova Scotia, New Brunswick, southern Quebec, southern Ontario and adjacent border states as far west as Minnesota (Sheviak and Brown 2002; NatureServe 2008*). In Ontario, the centre of its distribution, the species is ranked "apparently secure", the same rank that it has been assigned globally (S4, G4; Natural Heritage Information Centre 2008*; NatureServe 2008*). The species is considered "critically imperiled" in the three other Canadian provinces where it occurs (S1, NatureServe 2008*).

Spiranthes casei is a late-summer-flowering plant with up to 50 yellowish white flowers arranged in a single spiral on a flowering stem up to 49 cm high (Sheviak and Brown 2002, personal observations). The flowers are agamospermic and also bee pollinated (Catling and Catling 1991). Capsule production generally approaches 100% in eastern Ontario and western Quebec (Reddoch and Reddoch 1997). Like *S. magnicamporum* Sheviak and *S. cernua* (L.) L.C. Richard on the prairies (Sheviak 1991), *S. casei* is adapted to summer drought by having fugaceous basal leaves and descending, tuberous roots. Populations inhabit dry to moist, shallow to deep sands in old fields, grasslands, abandoned sand pits, open woodlands, roadsides and powerline corridors, and on acidic rock outcrops and ridges (Catling and Cruise 1974; Luer 1975; Brackley 1985; Whiting and Catling 1986; Case 1987; Reddoch and Reddoch 1997; Catling and Brownell 1999).

Little has been published on the population dynamics of the species. Case (1987) stated that in the western Great Lakes region *Spiranthes casei* was "a colonizer of disturbed sites, developing large populations briefly then waning rapidly." Reddoch and Reddoch (1997) described two long-lived populations in the Ottawa area. One population, in the Stony Swamp Conservation Area, Ottawa, Ontario, in 1996 had survived for at least 26 years in an area where the soil was too thin to support dense vegetation. This population is the major subject of the current study. The other population, in Gatineau Park, Quebec, 20 km to the north, in 1996 had persisted for at least 16 years in a field that had been mowed annually. After mowing was discontinued in about 2000, there was rapid succession to a young, dense White Pine (*Pinus strobus* L.) forest. We last found *S. casei* plants there in 2006. We also reported (Reddoch and Reddoch 1997) that populations on dry sites were particularly affected by drought and that, as a result, very few or no plants flowered in some years.

The European *Spiranthes spiralis* (L.) Chevall. is one of the few *Spiranthes* species for which population dynamics and flowering patterns have been studied over the long term (Kull 2002; Light and MacConaill 2005). This species has a phenology somewhat similar to that of *S. casei*, one significant difference being that all of the leaves of *S. spiralis* are produced in the fall (Wells 1967, 1981; Tatarenko and Kondo 2003). Wells (1981) followed an English population of *S.*

spiralis for 17 years, and Willems and colleagues (Willems 1989, 2002; Willems and Dorland 2000; Jacquemyn et al. 2007) a Dutch population for 24 years. These observers found that the number of plants changed somewhat from year to year, but that flowering was extremely variable. Both groups (Wells 1981; Jacquemyn et al. 2007) observed cohort half-lives of up to nine years. Wells (1981) concluded that conservation and management of orchid populations depend on an understanding of phenology and population dynamics, especially recruitment, mortalities, survivorship, and longevity of individual plants.

The goals of this study were to establish the life history, phenology, leaf production and longevity of *Spiranthes casei* plants in a population in the Stony Swamp Conservation Area, as well as their population and flowering dynamics. We also examined the longevities of this and seven other populations in the same conservation area. In the Mer Bleue Conservation Area, we followed a temporary colonization that possibly originated from a single plant. From our observations, we derived some implications for the conservation and management of *S. casei* populations.

Study Sites

Both study sites were in the National Capital Commission Greenbelt surrounding the urban core of the City of Ottawa, Ontario, on the lowlands of eastern Ontario. The climate is continental, with warm, moist summers and cold, snowy winters (Crowe 1984). The mean daily maximum and minimum temperatures over the 1971–2000 period were 26.5°C and 15.4°C in July, and -6.1°C and -15.3°C in January. The mean annual precipitation was 944 mm distributed fairly evenly throughout the year. The mean frost free period was about 159 days, extending, on average, from the beginning of May to early October (Environment Canada 2008*).

The major part of the work was done in the Stony Swamp Conservation Area (45°18'N, 75°49'W; 115 m above mean sea level), a 20 square km composite of second-growth forests, conifer plantations, marshes, beaver ponds, old fields, and scattered expanses of exposed, flat-lying bedrock. The bedrock is sandstone, interbedded with sandy dolomite in some places, of the Nepean and March formations (Wilson 1938; Bélanger and Harrison 1980). Within eastern Ontario and western Quebec close to Ottawa, *Spiranthes casei* is essentially concentrated in the Stony Swamp Conservation Area (Reddoch and Reddoch 1987, 1997).

The primary study site was a 1.4 ha opening of exposed sandstone surrounded by a second-growth forest dominated by *Acer saccharum* Marsh., *Fraxinus americana* L., *Quercus rubra* L., and *Pinus strobus* L. The opening is clearly visible in air photos back to 1945, the earliest coverage of the area available at the National Air Photo Library, Ottawa. The *Spiranthes casei* plants were spread along the northern edge of the opening within a strip about 200 m long and 50 m wide (Figures 1 and 2). They grew in thin layers of sand over bedrock or in cracks in the bedrock. A few specimens of the forest tree species and of the following species, *Acer rubrum* L., *Frangula alnus* Miller, *Populus grandidentata* Michx., *P. tremuloides* Michx., *Picea glauca* (Moench) Voss, and *Betula papyrifera* Marsh., were scattered across the opening. The most common shrub was *Juniperus communis* L. The most common grasses were *Danthonia spicata* (L.) Beauv. and *Panicum lanuginosum* Elliott var. *implicatum* (Scribner) Fernald. Rosettes of the latter made it difficult to distinguish the similarly sized and shaped juvenile/immature plants and emerging leaves of *S. casei*. *Vaccinium angustifolium* Ait. and *V. myrtilloides* Michx. were the most frequent companion plants. Other herbs that occurred within 50 cm of *S. casei* plants were *Rumex acetosella* L., *Hypericum perforatum* L., *Hieracium caespitosum* Dumort. ssp. *caespitosum*, *Packera paupercula* (Michx.) A. Löve & D. Löve, *Solidago nemoralis* Ait., and, occasionally, *Cypripedium acaule* Ait., *Malaxis unifolia* Michx., *Spiranthes lacera* (Raf.) Raf. var. *lacera*, and *Spiranthes cernua*.

The second study site was in the Mer Bleue Conservation Area (45°24'N, 75°31'W; 75 m above mean sea level), 25 km east of the Stony Swamp Conservation Area, at a location that we have frequented since 1966 while monitoring a population of *Spiranthes cernua* there (Reddoch and Reddoch 1997). In 1966 the site was part of a large, recently abandoned borrow pit of well-drained sand that was devoid of vegetation; currently it is somewhat shaded by well-spaced *Populus tremuloides* trees that lost some of their canopy in the January 1998 ice storm (Figure 3). In the vicinity of the *S. casei* plants were several *P. tremuloides* saplings up to 1 m high. The ground cover included *Danthonia spicata*, *Trifolium repens* L., *Packera paupercula*, and *Polytricum* mosses. The shade and deep sand distinguish this habitat from those at Stony Swamp. At both sites, the substrates were acidic sands of pH 4.0–4.5 (Reddoch and Reddoch 1997).

Materials and Methods

Guided by a mixed specimen sheet of *Spiranthes casei* and *S. cernua* at the Vascular Plant Herbarium, Agriculture and Agri-Food Canada (DAO), collected by C. and E. Frankton (#2385) in 1972, we relocated *S. casei* (and *S. cernua*) at the collection site in the Stony Swamp Conservation Area in 1977 (Reddoch and Reddoch 1997). From then on we monitored *S. casei* flowering plants on an infrequent basis at this and seven other populations in the Conservation Area. The populations were 100–500 m in extent. The location of the 1972 collection became our primary study site in 2002 when we initiated a detailed examination of all plants encountered. We continued to check the other Stony Swamp populations from time to time until 2008.

FIGURE 1. The central portion of the Stony Swamp Conservation Area study site. Note the deer browse line on the trees. Photograph taken 23 August 2008. All photographs by Joyce Reddoch.

At the Stony Swamp study site between 2002 and 2008, we followed a total of 152 individuals (genets and ramets) of *Spiranthes casei*: 112 mature individuals and 40 juvenile/immature individuals. Of the mature individuals, only six were within 5 cm of other individuals and could possibly be interpreted as vegetative offshoots (ramets). Because these possible offshoots represented only 4% of the population, we did not distinguish between genets and ramets in this paper. For the most part, plants were detected initially when they were in flower. Juvenile/immature plants were discovered only occasionally when they were in the vicinity of established plants. We made three visits between the beginning of May and the end of June to measure and count leaves, and two trips in July (and sometimes one in early August) to record the appearance and condition of flowering shoots/stems. We returned at flowering time in August to count flowers, to measure flowering stems, and to record their condition and the occurrence of deer herbivory. We came back again at seed release time at the beginning of October to note surviving reproductive stems, and before freeze-up in early to mid-November to measure and mark the leaves of the fall rosettes. We measured the first two leaves on fall rosettes between 2005 and 2008 (n = 253 fall rosettes) and all available third to seventh leaves (n = 210) in 2005 and 2006. We made total leaf counts between 2005 and 2008. The graphs were based on the data derived from the Stony Swamp population; data collection concluded in November 2008.

In 1998 we discovered a flowering plant of *Spiranthes casei* at the Mer Bleue site and began to track it, as well as the total of 14 juvenile/immature plants that appeared in a 1 m^2 area adjacent to and south of it. We visited this site following the same protocol and schedule as at Stony Swamp.

At all locations we took care to walk only on exposed bedrock or along designated routes to avoid altering the habitat or stepping on juvenile/immature and vegetative plants. We mapped the plants and marked them by bracketing each one with small plastic rods that could be removed at the end of the study. We kept track of the leaves by numbering each one with a system of dots made with a fine-point permanent marker.

In 1979 and 1986, we collected a total of 40 flowering and vegetative plants of *Spiranthes casei* ahead of residential development in the Bridlewood subdivision adjacent to the western boundary of the Stony Swamp Conservation Area. We deposited representative herbarium sheets at the Vascular Plant Herbarium, Agriculture and Agri-Food Canada (DAO), and examined all specimens held by that herbarium and the National Herbarium of Canada (CAN). These specimens provided information on the morphology of juvenile/immature plants, as well as of the tuberous roots, and fall shoots/buds of flowering and vegetative plants.

Records of temperature and precipitation (Environment Canada 2008*) originated at the Macdonald-Cartier (Ottawa) International Airport weather station (elevation 114 m above mean sea level), which is about 12 km from each study site. Vascular plant nomenclature followed that of the Ontario Natural Heritage Information Centre (2008*), except that Dore and McNeill (1980) was used for grasses.

Corel Quattro Pro X3 provided descriptive statistics, *t*-tests, ANOVA (analysis of variance), and regression analysis. In addition, a more generalized program was set up in Quattro to do ANOVA with samples of unequal size following, in part, Sokal and Rohlf (1994). Half-lives were obtained by linear regression analysis of log-transformed annual population counts of marked plants.

Results

Life History

We encountered seven life history stages: seed/protocorm, juvenile, immature, flowering, vegetative, non-emergent, and offshoot (Figure 4). Some of these stages could be assigned with confidence only after the plants had been followed for a number of years. The interface between juvenile and immature stages was not clear-cut. We define the juvenile stage as the initial leafy stage of plant growth that lasted one year (Figure 5). The subsequent immature stage continued to develop over several years until the plant flowered. A mature plant is one that is in flower or has flowered, and can be flowering, vegetative or non-emergent in a given year.

Offshoots were defined to be those individuals that appeared within 5 cm of another individual, either from flowering or vegetative plants. Since it was seldom possible to determine unambiguously whether new individuals in the vicinity of mature plants were offshoots or juvenile plants, we use the term "plant" to mean any individual, whether genetically related to other individuals or not. We reported previously (Reddoch and Reddoch 1997) that vegetative reproduction, as expressed by pairs or clumps of individuals, was insignificant in this species in the Ottawa area. In this study, there were six mature plants (genets) with a mature putative offshoot (ramet) within 5 cm and an additional six mature plants with immature putative offshoots. Vegetative reproduction in other *Spiranthes* species occurred by the production of a bud on the underground stem or at the root tip (Catling 1989). The former is the more likely form of vegetative reproduction in *S. casei* because most of the putative offshoots were within one cm of the original plant.

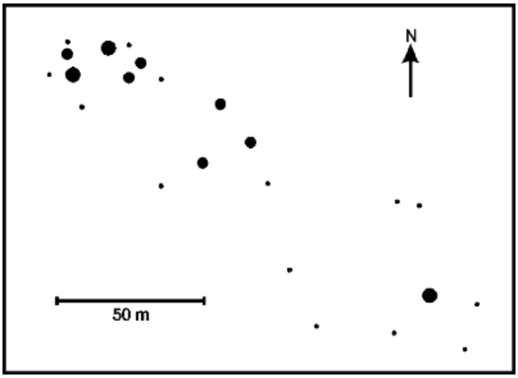

FIGURE 2. Map of the distribution of all *Spiranthes casei* plants studied at the Stony Swamp site. Small dots represent 1–4 individuals, medium dots 5–10 individuals, and large dots 20–25 individuals.

Phenology and Leaf Production

Except as noted, this section is based on our observations of *Spiranthes casei* plants in the field, on our collected specimens, and on herbarium specimens. The aerial part of next year's growth began as a lanceoloid shoot appearing above ground at anthesis (Mousley (1924, sub *S. cernua* var. *ochroleuca*), Reddoch and Reddoch 1997). The shoots of vegetative plants initiated their development up to a month earlier than those of flowering plants. Plants with flowering stems that had dried up or had been decapitated accidentally before flowering also produced their shoots earlier than plants that supported intact flowering stems (Reddoch and Reddoch 1997). In *S. spiralis*, also, the leaves of vegetative plants appeared earlier than those of flowering plants (Wells 1981).

TABLE 1. Mean annual leaf numbers on fall rosettes of plants that had been vegetative, of plants that had flowered, and of the combined vegetative and flowering plants. (SE = standard error.)

		2005	2006	2007	2008
Vegetative	mean ± SE	2.31 ± 0.12	1.72 ± 0.14	2.03 ± 0.08	2.26 ± 0.08
	number	29	29	58	42
Flowered	mean ± SE	1.82 ± 0.16	1.23 ± 0.12		1.83 ± 0.14
	number	22	47		23
Combined	mean ± SE	2.10 ± 0.10	1.42 ± 0.09	2.03 ± 0.08	2.11 ± 0.08
	number	51	76	58	65

FIGURE 3. Habitat of the temporary colonization in the Mer Bleue Conservation Area in 1998. The founder plant is circled. The trees in the background show the effects of the January 1998 ice storm. Photograph taken 23 August 1998.

During September and October, the shoots developed into rosettes of two (occasionally one, three or four) leaves with a growing tip in the centre (Figure 6, Table 1). Plants that had flowered that summer sometimes produced only a growing tip. The first and second leaves were generally ovate in shape and were 0.2–2.5 cm wide and 0.2–3.5 cm long. Mean lengths (± standard error) for the first two leaves (2005–2008) were 1.21 ± 0.05 cm, $n = 190$, and 1.97 ± 0.05 cm, $n = 161$, respectively.

Fall rosettes had more leaves on plants that had been vegetative that summer than on those that had flowered (Table 1). In 2005, 2006, and 2008, there were significantly more leaves on the fall rosettes of plants that had been vegetative (*t*-tests: $t_{2005} = 2.5$, $P < 0.02$, df = 49; $t_{2006} = 2.6$, $P < 0.01$, df = 74; $t_{2008} = 2.9$, $P < 0.01$,

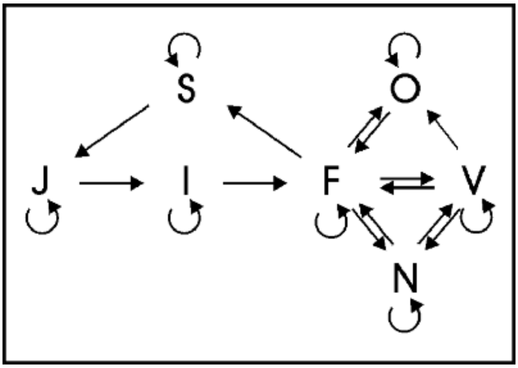

FIGURE 4. Life history diagram of *Spiranthes casei* in eastern Ontario. Arrows represent annual transitions between stages; S = seed and protocorm, J = juvenile, I = immature, F = flowering, V = vegetative, N = non-emergent, and O = offshoot (ramet) stages. The arrows directed upward to seed and offshoot stages represent reproductive transitions.

FIGURE 5. A juvenile *Spiranthes casei* plant in the Stony Swamp Conservation Area. The length of the second leaf, on the left, was 2.3 cm. Photograph taken 24 July 2006.

df = 63). A comparison in 2007 was not meaningful because only two plants flowered. The rosettes overwintered under the snow; the first two leaves generally did not grow further in the spring except on late-developing rosettes.

In the spring, vegetative plants continued on to produce a total of 3–6 leaves (occasionally 2; once 9 at the Mer Bleue site), while flowering plants had a total of 5–6 (occasionally 4 or 7) leaves (Figure 7). By late May, the third leaf had reached its final size, with lengths of 3.0–9.5 cm and widths of 1.0–1.9 cm. The fourth, fifth and sixth leaves had finished growing by the beginning of July with lengths of 6–15 cm and widths of 1.0–1.8 (rarely to 2.1) cm. The seventh leaf, when it occurred, continued to grow until mid-July, into a similar size range. These leaves were oblanceolate to linear-lanceolate, arranged in sub-opposite pairs, each pair at right angles to the previous pair. At the beginning of July, the original pair of leaves had turned yellow to brown or had already disappeared. During July, depending on the temperature and precipitation, the remaining leaves remained green or became brown at their tips or turned entirely brown. Thus it was difficult to find intact leaves on which their maximum lengths could be measured. Usually all of the basal leaves were brown at anthesis.

In a plant that was preparing to flower, the growing tip of the flowering stem was evident in late June to early July and continued to extend and develop through July and August. There were usually four (range three to five) cauline bracts, the upper ones appressed and the basal one or two often wide-spreading and leafy. These basal-cauline leafy bracts were sometimes still green at anthesis, long after the basal leaves had become brown and shriveled. The buds were clearly visible by early August, arranged in three vertical or slightly twisted ranks, spiraling upwards opposite to the direction that the flowers were going to face. At anthesis, between mid-August and early September, there were generally six flowers per turn in one long spiral. The flowering stems were 8.5–46.5 cm high (mean 24.4 ± 0.51 cm, n = 138), inflorescence heights were 3–16.5 cm high (mean 7.7 ± 0.23 cm, *n* = 119), and there were 4–45 flowers/inflorescence (mean 20.9 ± 0.68, n = 129 inflorescences). Seed capsules dehisced and released seed throughout October.

Mousley (1942; sub. *Spiranthes vernalis*) reported that the buds of the first pair of tuberous roots for the next year were evident in late September. We found that such root-buds had not developed further by mid-April, and confirmed Mousley's observation (Mousley 1924; sub *S. cernua* var. *ochroleuca*) that the early stages of root expansion were present in mid-May. At anthesis, we noted that the crisp, white, descending roots of the year extended down over the soft, brownish roots of the previous year.

To discover whether there was a relationship between the total number of basal leaves and the probability of a mature plant flowering, we marked and counted the basal leaves on all available mature plants between 2005 and 2008. We found that plants with two or three leaves were always vegetative, while plants with four, five or six leaves were either vegetative or flowering

FIGURE 6. A fall rosette of a *Spiranthes casei* plant in the Stony Swamp Conservation Area. The first leaf, right, was 1.7 cm long, and the second leaf, left, was 2.2 cm long. Photograph taken 1 November 2008.

(Figure 7). Flowering plants had five or six (rarely four or seven) leaves, and a quarter to almost a half of vegetative plants also had five or six leaves. Except in 2007, a plant with five leaves had a 43% to 66% probability of flowering, and one with six leaves a 56% to 75% probability. The probability of a plant with seven leaves flowering was 100%. An exception to the rule that the more leaves on a mature plant the more likely it is to flower occurred one year at the Mer Bleue site when the mature plant there produced nine leaves while remaining vegetative (see above).

Juvenile plants had three leaves (Figure 5); immature plants produced up to 5 (rarely 6) leaves that were up to 9 cm long. Immature plants followed the same pattern of leaf production as vegetative plants.

Population Dynamics

In this section and a following section on flowering dynamics, we present the data derived from the Stony Swamp study site in two datasets. The first dataset shows the annual changes in the marked mature plants that we followed from year to year through the growing seasons (Figures 8a and 10a). The second dataset provides a summary of the annual demographic information on all of the mature plants in the population, i.e., the marked plants and the newly-found plants (Figures 8b and 10b). In addition, we report observations on the juvenile and immature plants that we encountered by chance while monitoring the mature plants.

The marked mature plants yielded annual information on the total number of such plants, the number that were consumed by gastropods before the flowering stems could emerge in early July, the number of surviving plants that initiated flowering stems, the number that remained vegetative, and the number that were non-emergent. This information is presented in Figure 8a and expanded on below.

Gastropods included both slugs and snails, especially the conspicuous Banded Wood Snail (*Cepaea nemoralis* Linnaeus). Each year, gastropod damage was evident on the leaves of many plants. However, in addition, gastropods consumed all of the above-ground parts of some plants, including an unknown number of potential flowering stems. Such complete gastropod herbivory between 2003 and 2008 ranged from 6% of the plants in 2005 to 39% in 2008, the six-year mean being 17% (Figure 8a). The high percentage of gastropod herbivory in 2008 was likely the result of exceptionally wet summer weather (Environment Canada 2008*) when frequent, often light, rain kept the ground wet from June to early August (personal observation) and provided ideal conditions for gastropod activity. Of the total of 31 mature plants that sustained gastropod herbivory between 2003 and 2007, eight died the

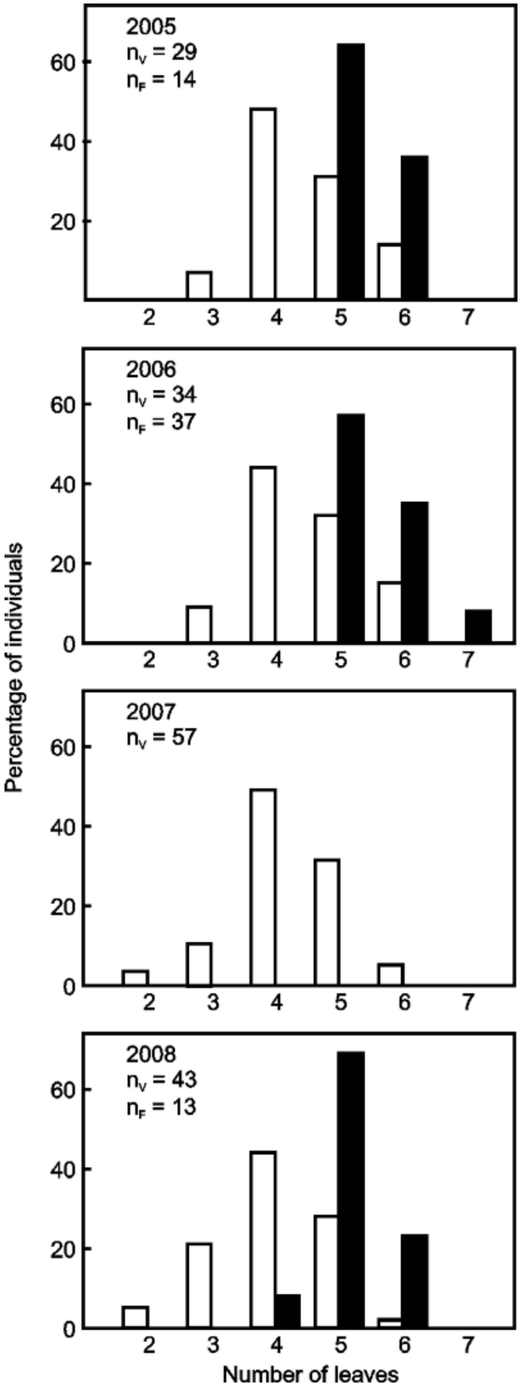

FIGURE 7. The distribution of the number of basal leaves of mature vegetative (white bar) and flowering (black bar) plants (2005–2008). Percentages represent leaves on vegetative and flowering plants separately. There were only two flowering plants in 2007, one each with four and five leaves (not plotted).

year following herbivory, six flowered, one did not emerge (see below) and the rest remained vegetative.

In addition to gastropod herbivory, weevils (*Stethobaris ovata* (LeConte, 1868)) damaged the leaves of several *Spiranthes casei* plants. Two specimens were collected on 13 June 2008 and deposited in the Canadian National Collection of Insects, Ottawa. *Stethobaris ovata* is known to feed on a number of orchids in North America (Howden 1995; Dunford et al. 2006); this appears to be the first record of its occurrence on *Spiranthes*.

Initiation of flowering stems in the marked mature plants that survived gastropod herbivory varied between 18% of the total marked mature plants in 2008 and 49% in 2006 (Figure 8a). These values exclude the exceptionally low-flowering year of 2007, when only two plants flowered, and the unrealistically high value of 90% in 2002 that reflected our lack of awareness of existing vegetative plants at the beginning of the study.

Non-emergence was an infrequent occurrence (Figure 8a). Between 2003 and 2008, a total of seven mature plants did not emerge for one year each, while one additional mature plant did not emerge for two consecutive years. The life stages before and after non-emergence (using a hyphen for a non-emergent year, F for a flowering year and V for a vegetative year) were as follows: three V–V, two F–V, one V–F, one F–F, and one F– – F. One of the plants that was non-emergent between two vegetative years had been eaten by gastropods in the initial year (see above). Two immature plants also were non-emergent for one year. Only one of the mature plants that had been non-emergent has since died. Non-emergence did not appear to be a symptom of senescence as it was for the tuberous orchid *Platanthera hookeri* (Reddoch and Reddoch 2007a).

Overall, the total number of mature plants observed increased annually for the first four years of the study (Figure 8b), likely reflecting our growing knowledge of the population, particularly in the first two years. The increase in numbers came from the annual addition of new flowering plants. Between 2004 and 2008, the new flowering plants contributed 40% to 55% of the annual total of flowering plants and 15% to 25% to the annual total of mature plants. In 2007 there were no new flowering plants.

The total number of juvenile/immature plants present during the study was not known because they were so difficult to find. Of the 40 juvenile/immature plants that we did discover, we were able to follow only two of them from first emergence to flowering. One of them flowered three years after first emergence and the other flowered after two years. Other juvenile/immature plants persisted for up to six years after emergence without flowering. Using asymbiotic culture of several batches of *Spiranthes casei* seeds from the Stony Swamp Conservation Area, Marilyn Light (per-

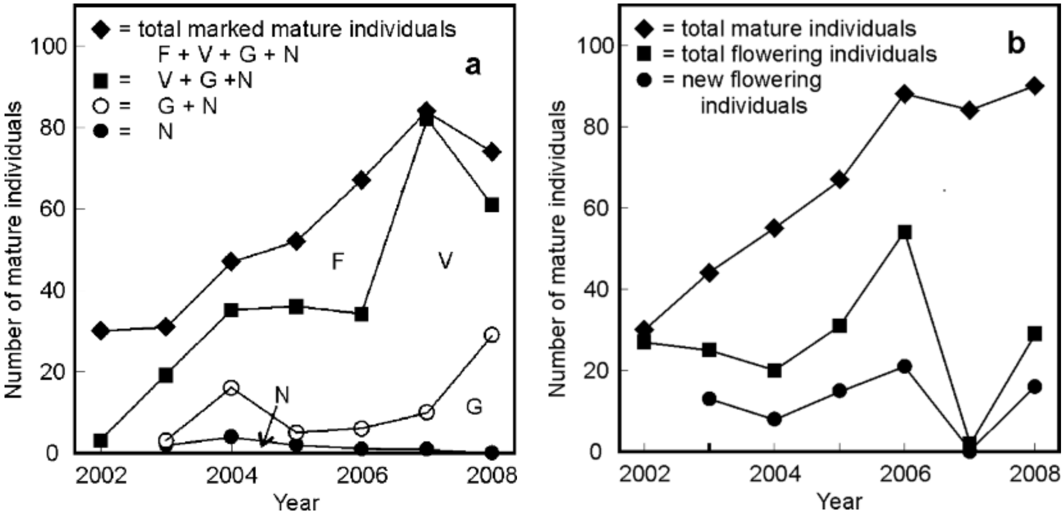

Figure 8. Population dynamics (2002–2008). a) The annual stage distributions of marked mature plants: F = initiated flowering stems, V = vegetative, and N = non-emergent. G = plants eaten by gastropods before intent to flower was evident. b) The annual counts of total mature plants and of total flowering plants. The annual counts of newly-discovered flowering plants are also shown.

sonal communication) observed some swollen embryos within a month of sowing and 0% to 95% germination two months later. Six months after sowing, the germinated seeds had produced small plants with three green leaves, the third one not completely unfurled. This rate of asymbiotic development is comparable to that observed for *S. cernua* (Stoutamire 1964), *S. lacera* (sub *S. gracilis*) and *S. romanzoffiana* Cham. (Oliva and Arditti 1984), and *S. spiralis* (Wells and Kretz 1983).

Mortality of juvenile and immature plants appeared to be quite high; for example, of the 26 known juvenile/immature plants present in 2007, only seven reappeared in 2008.

Plant and Population Longevities

One of the goals of this study was to determine a range of lifetimes for individual mature plants as well as for populations; however, it is now apparent that the average lifetimes of the mature plants in this population were longer than the extent of the study. Of the 30 mature plants recorded at the Stony Swamp study site in 2002, 19 (63%) were still alive in 2008. Three of those plants had been known since 2001 and one since 1998. Of the increased total of 42 mature plants present in 2003, 29 (69%) were still extant in 2008. In Figure 9, the annual numbers of mature plants for the 2002 and 2003 datasets are shown as depletion curves on a semi-log plot. These two depletion curves yielded essentially identical half-lives for mature plants of 9.48 ± 0.69 and 9.41 ± 0.46 years, respectively, which are equivalent to mean lifetimes (half-life/ln 2) of 13.7 and 13.6 years.

Including the study site which is the subject of this paper, all eight populations of *Spiranthes casei* in the Stony Swamp Conservation Area that were first recorded between 1972/1981 and 2008 were still extant. The majority of the plants were in sandstone barrens that remained relatively unchanged because the shallow sandy soil inhibited succession (Reddoch and Reddoch 1997). In 2008, some additional plants persisted in remnant openings among secondary forest growth adjacent to the open barrens. Generally, then, *Spiranthes casei* populations can persist for more than three decades in relatively stable habitats.

Temporary colonization

In September, 1998, in the Mer Bleue Conservation Area, we encountered for the first time a single flowering plant of *Spiranthes casei* at the southern edge of a *S. cernua* population that we had been monitoring for a number of years. Since we knew the area very well, we were fairly certain that this was the first time that a *S. casei* plant had flowered there. The plant flowered again in 2000 but did not flower again. In an area 1 m square to the south of the original plant, we discovered six juvenile/immature plants in 1999, six more in 2000, one in 2003, and one more in 2007. The first 13 juvenile/immature plants died within four years, the mean survival time after we discovered them being three years. In 2008, two plants remained, the original plant and the immature plant discovered in 2007. If there were no other *S. casei* populations closer than those at Stony Swamp, it is possible that we were the inadvertent vectors carrying the seed(s) to this locality.

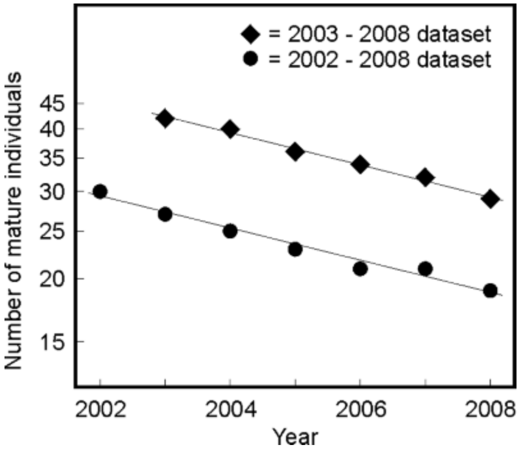

FIGURE 9. Depletion curves for the mature plants that were present in 2002, and that were present in 2003, on a semi-log scale. The lines were derived from least-squares fits of ln n vs. time.

Flowering Dynamics

For the marked plants (Figure 10a), hot summer weather between early July, when flowering stem shoots first appeared, and mid-August, when the flowers began to open, caused some of the developing flowering stems to dessicate and shrivel. Between 2002 and 2006, the proportion of dessicated stems ranged from 17% in 2004, when July and August temperatures were slightly below the 30-year normal, to 56% in 2005, when July and August temperatures were 1.6°C above normal. Rainfall in both years was close to normal (Environment Canada 2008*). The mean loss to dessication for the period 2002–2006 was 41%. Neither of the two flowering stems present in 2007 dried up, nor did any of the 13 flowering stems in the wet, cool summer of 2008.

During the course of this study, we frequently observed White-tailed Deer (*Odocoileus virginianus*) at the study site and elsewhere in Stony Swamp, reflecting the widespread problems of high deer densities in Eastern Ontario and Stony Swamp in particular (Broadfoot and Voit 2000*, Widenmaier and Fahrig 2006*). At the study site between 2000 and 2005, a deer browse-line developed at a height of 1.5 m on the trees both in the opening and throughout the surrounding forest (see Figure 1), and our deer sightings became more common. Deer herbivory of *Spiranthes casei* stems began when some of the flowers were open and was evidenced by the shredded tip of the remaining part of the stems. Annual herbivory by White-tailed Deer of the marked inflorescences between mid-August and early October ranged from 8% in 2008 to 67% in 2003 (Figure 10a). The mean deer herbivory over the years 2002–2008 was 33%. The percentage of marked flowering stems that survived to produce seed in early October ranged from 0% in 2002 to 92% in 2008.

At anthesis in late August, the total number of flowering stems in the field was the sum of the marked stems that survived to flowering and the newly-discovered stems (Figures 8b, 10b). Annual White-tailed Deer herbivory of the total flowering stems present in August ranged from 18% in 2006 to 77% in 2003 (Figure 10b). Overall, then, the percentage of all flowering stems that produced seed between 2003 and 2008 ranged from 23% in 2003 to 82% in 2006, the six-year mean being 56%. The year 2002 had one of the hottest, driest summers on record with half of the normal July and August precipitation and with temperatures 1.3°C above normal (Environment Canada 2008*). Under these conditions, 33% of the 27 flowering stems observed that year dried up even during anthesis. In the years 2003 to 2006, some flowering stems dried up while expanding in July and August, but not at anthesis (see above).

The year 2007 was exceptional for the small number of plants that flowered (Figures 8 and 10). The plants of 2007 developed from fall rosettes that formed in September and October of 2006. These 2006 fall rosettes had significantly fewer leaves than those that formed in 2005, 2007 and 2008 (Table 1; ANOVA $F_{[3,246]} = 15.4$, $P < 0.001$). Taken separately, the fall rosettes of vegetative and flowering plants also had significantly fewer leaves in 2006 (Table 1; ANOVA $F_{[3,154]} = 5.6$, $P < 0.002$; ANOVA $F_{[3,89]} = 6.9$, $P < 0.002$, respectively).

One factor that could have contributed to smaller fall rosettes in 2006 was the exceptionally high September and October precipitation, which was 170% of normal. In addition, more rain implies more cloudy weather as well as less sunshine and warmth. In fact, the mean number of hours that were "Clear" or "Mainly Clear" between 8 a.m. and 4 p.m. Eastern Standard Time in September and October of 2006 (1.9 hrs/day) was significantly less than in the same period of 2005 (3.5 hrs/day), 2007 (3.6 hrs/day), and 2008 (3.1 hrs/day; Environment Canada 2008*; ANOVA $F_{[3,240]} = 3.4$, $P < 0.02$).

Flowering patterns of individual plants were highly variable. Of the 24 mature plants present for the five years 2002–2006, 50% flowered twice, 17% once, and 17% three times. Two of the plants flowered every year but one, and two flowered all five years. For the whole population, 54% of the mature plants flowered consecutively for at least two years between 2002 and 2006.

Discussion

Long-term studies are essential for understanding the behaviour of orchid populations (Kull 2002; Light and MacConaill 2005; Pfeifer et al. 2006; Jacquemyn et al. 2007; Reddoch and Reddoch 2007a, 2007b). Ideally such studies should last at least as long as the average lifetimes of the individual plants. Studies lasting two or more decades may be necessary to acquire a comprehensive picture of the population and to find

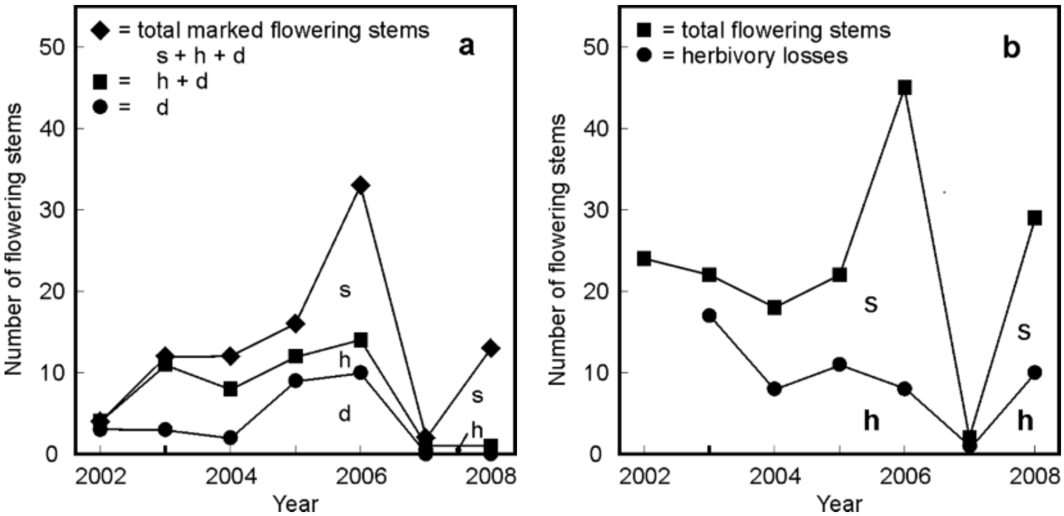

FIGURE 10. Flowering dynamics (2002–2008). a) The annual fates of the marked flowering stems from emergence in July until seed dispersal in October, showing the stems lost to drought (d) and to deer herbivory (h), and the stems that survived to disperse seed (s). b) The annual losses to deer herbivory of all of the flowering stems present at flowering time from mid-August until seed dispersal in October (h), and the flowering stems that survived to disperse seed (s).

correlations of population and flowering dynamics with external factors such as weather. But even a seven-year study of a species such as *Spiranthes casei*, with a mean mature plant lifetime of 13.7 years, can yield some useful insights.

The populations of *Spiranthes casei* in the arrested subclimax conditions of the Stony Swamp Conservation Area have persisted for more than three decades. Individual mature plants that were present in the study area in 2002 and in 2003 yielded half lives of about 9.4 years, a value close to the half-life range of 4.6–9.2 years found for annual cohorts of *S. spiralis* (Wells 1981, Jacquemyn et al. 2007). Seeding, rather than vegetative reproduction, was the main source of new plants and thus of the continuity of the populations. The temporary colonization of the rapidly-changing seral community at the Mer Bleue Conservation Area seems to depend on one individual, which has been present as a mature plant for at least 11 years. It is likely that plant lifetimes are dependent on the stability of their habitats, and, therefore, that plant lifetimes at the Mer Bleue Conservation Area would be different from those at Stony Swamp.

There are a number of factors that affect whether a mature *Spiranthes casei* plant will produce flowers. The more leaves on a plant, the greater the probability of it flowering. This observation is consistent with the behaviour of other tuberous orchids, for example, *Ophrys apifera* Hudson (Wells and Cox 1989) and *Himantoglossum hircinum* Spreng. (Pfeifer et al. 2006). After flowering, the fall rosettes of flowering plants developed later and had significantly fewer leaves than did plants that had been vegetative, suggesting that flowering did have an impact on the plants' resources. In addition, though, since all fall rosettes, from both flowering and vegetative plants, were smaller in 2006 than in other years, the decrease in 2006 was not a consequence of the large flowering (62%) that year but rather had other causes.

It is not clear whether flowering one year reduces the probability of flowering again the next year. About half of the mature plants of *Spiranthes casei* in the Stony Swamp study area flowered consecutively for at least two years in a five-year period, while the Mer Bleue individual flowered only twice, in non-consecutive years. By comparison, in Nebraska, two-thirds of the *S. cernua* plants in a population that had been studied for nine years flowered for at least two consecutive years (Antlfinger and Wendel 1997), while only 15% of a Dutch *S. spiralis* population did so during an 18-year study (Willems and Dorland 2000).

Fall weather appears to have a considerable influence on whether mature plants will flower or not in the following year. In *Spiranthes casei*, reduced exposure to sunlight during the time of rosette development in the fall of 2006 was followed by significantly smaller fall rosettes and almost no flowering in 2007. Here, the resource being limited was the energy required for photosynthesis, and also, perhaps, for triggering flower formation. In addition, the preference of *S. casei* for well-drained sites suggests that extended periods of very high rainfall could have a direct negative impact on development. Thus, the very high rainfall, combined with much less sunshine, may have led to smaller fall rosettes, and, consequently, to significantly fewer flowering plants in the following year. Summer weather was a factor in determining whether flowering stems, once initiated, reached the flowering state (Figure 10a). Rock barrens and open areas of well-drained sand are particularly susceptible to drought in hot, dry summers.

Herbivory can have a serious impact on *Spiranthes casei* plants. Gastropods not only ate parts of leaves but also killed both juvenile/immature and mature plants. Prolonged periods of wet weather in May and June could allow gastropods to have a serious impact on a population. White-tailed Deer have become an increasing problem in the Stony Swamp Conservation Area since about 2000 (Widenmaier and Fahrig 2006*; personal observations). Deer ate the *S. casei* flowers, thus reducing the annual seed production, but did not directly kill any plants. The long-term effects of deer herbivory are difficult to predict.

In summary, then, there were several external factors, acting separately or in combination, that resulted in reduced flowering. Damp, cloudy, fall weather reduced the sizes of the fall rosettes. Damp, cloudy, early summer weather enhanced gastropod activity that eliminated above-ground parts of some plants; hot, dry summers dessicated some developing flowering stems; and deer consumed some inflorescences once they had formed. The impact of damp weather depended not so much on how much rain fell but rather on how continuously damp, cloudy conditions occurred.

This study shows that the censuses required for sound management of orchid populations such as *Spiranthes casei* must be preceded by extensive and intensive fieldwork. A one-time census at flowering time is of limited value besides confirming that the population is "still there". Even annual censuses of flowering stems do not give a realistic idea of the population size or trends because these counts can vary dramatically from year to year as a result of different weather effects and herbivory. In addition, vegetative and non-emergent plants are not visible at flowering time to be counted. Thus the management goals for a population should include ongoing tracking of all plants in a suitably large sampling area. As well, habitats must be maintained in an early stage of succession if this is not the natural consequence of shallow soils. Annual mowing late in the fall after seed release or very early in the spring before leaf growth begins is essential for controlling woody plants. Adequate drainage and a suitable moisture regime also must be maintained.

Acknowledgments

We are grateful to the National Capital Commission for permits to conduct this research in the Greenbelt; Stephen Darbyshire, Agriculture and Agri-Food Canada, for identifying a grass; Patrice Bouchard, at the same institution, for confirming the identity of the *Stethobaris* species; Jane Topping, formerly at the Canadian Museum of Nature, for providing information on Banded Wood Snails; Marilyn Light for germinating seeds from a Stony Swamp population and providing useful references; and two reviewers for their comments and suggestions.

Documents Cited (marked * in text)

Bailey, R. G. 1998. Ecoregions map of North America: explanatory note. Miscellaneous publication 1548. USDA Forest Service, Washington, D.C. 10 p. + map.

Broadfoot, J. D., and **D. R. Voit**. 2000. The status of deer herds in the western Greenbelt of the National Capital and recommendations for their management. National Capital Commission and Department of National Defence, Ottawa, Ontario.

Environment Canada. 2008. National Climate Archive. Environment Canada, Ottawa, Ontario. http://climate.weatheroffice.ec.gc.ca/.

Natural Heritage Information Centre. 2008. List of Ontario species. Vascular Plants. *Spiranthes casei*. Ontario Ministry of Natural Resources. http//nhic.mnr.gov.on.ca/MNR/nhic/species/species_list.cfm.

NatureServe. 2008. NatureServe Explorer: *Spiranthes casei*. NatureServe, Arlington, Virginia. http://www.natureserve.org/explorer.

Widenmaier, K., and **L. Fahrig.** 2006. Inferring White-tailed Deer (*Odocoileus virginianus*) population dynamics from wildlife collisions in the City of Ottawa. Pages 589–602 *in* Proceedings of the 2005 International Conference on Ecology and Transportation. *Edited by* C. L. Irwin, P. Garrett, and K. P. McDermott. Center for Transportation and the Environment, North Carolina State University, Raleigh, North Carolina. http://repositories.cdlib.org/jmie/roadeco/Widenmaier2005a.

Literature Cited

Antlfinger, A. E., and **L. F. Wendel.** 1997. Reproductive effort and floral photosynthesis in *Spiranthes cernua* (Orchidaceae). American Journal of Botany 84: 769–780.

Bélanger, J. R., and **J. E. Harrison.** 1980. Regional geoscience information: Ottawa-Hull. Geological Survey of Canada, Ottawa, Ontario. Paper 77-11. Text and maps.

Brackley, F. E. 1985. The orchids of New Hampshire. Rhodora 87: 1–117.

Case, F. W., Jr. 1987. Orchids of the Western Great Lakes Region. Revised edition. Cranbrook Institute of Science, Bloomfield Hills, Michigan. Bulletin 48. 251 pages.

Catling, P. M. 1989. Biology of North American representatives of the subfamily Spiranthoideae. Pages 49–67 *in* A conference: North American native terrestrial orchid propagation and production. Brandywine Conservancy, Pennsylvania.

Catling, P. M., and **V. R. Brownell.** 1999. The flora and ecology of southern Ontario granite barrens. Pages 392–405 *in* Savannas, barrens, and rock outcrop plant communities of North America. *Edited by* R. C. Anderson, J. S. Fralish, and J. M. Baskin. Cambridge University Press, Cambridge U.K. 480 pages.

Catling, P. M., and **V. R. Catling.** 1991. A synopsis of breeding systems and pollination in North American orchids. Lindleyana 6: 187–210.

Catling, P. M., and **J. E. Cruise.** 1974. *Spiranthes casei*, a new species from northeastern North America. Rhodora 76: 526–536.

Crowe, R. B. 1984. The climate of Ottawa-Hull. Climatological Studies Number 35. The Climate of Canadian Cities Number 1. Environment Canada, Ottawa, Ontario. 42 pages.

Dore, W. G., and **J. McNeill.** 1980. Grasses of Ontario. Monograph 26. Research Branch, Agriculture Canada, Ottawa, Ontario. 566 pages.

Dunford, J. C., D. K. Young, and **S. J. Krauth.** 2006. *Stethobaris ovata* (LeConte) (Curculionidae) on Eastern Prairie Fringed Orchid [*Platanthera leucophaea* (Nuttall) Lindley] in Wisconsin. Coleopterists Bulletin 60: 51–52.

Howden, A. T. 1995. Structures related to oviposition in Curculionoidea. Memoirs of the Entomological Society of Washington 14: 53–102.

Jacquemyn, H., R. Brys, M. Hermy, and **J. H. Willems.** 2007. Long-term dynamics and population viability in one of the last populations of the endangered *Spiranthes spiralis* (Orchidaceae) in the Netherlands. Biological Conservation 134: 14–21.

Kull, T. 2002. Population dynamics of north temperate orchids. Pages 139–165 *in* Orchid biology: reviews and perspectives, VIII. *Edited by* T. Kull and J. Arditti. Kluwer Academic Publishers, Amsterdam, The Netherlands.

Light, M. H. S., and **M. MacConaill.** 2005. Long-term studies: a case for orchid species survival. Selbyana 26: 174–188.

Luer, C. A. 1975. The native orchids of the United States and Canada excluding Florida. New York Botanical Garden, New York. 361 pages.

Mousley, H. 1924. Further notes on the underground development of *Spiranthes romanzoffiana* and *S. cernua*. Orchid Review 32: 296–300.

Mousley, H. 1942. The spring Ladies' Tresses (*Spiranthes vernalis* Engelm. & Gray) in Canada. Canadian Field-Naturalist 56: 1–2.

Oliva, A. P., and **J. Arditti.** 1984. Seed germination of North American orchids. II. Native California and related species of *Aplectrum*, *Cypripedium*, and *Spiranthes*. Botanical Gazette 145: 495–501.

Pfeifer, M., W. Heinrich, and **G. Jetschke.** 2006. Climate, size and flowering history determine flowering pattern of an orchid. Botanical Journal of the Linnean Society 151: 511–526.

Reddoch, J. M., and **A. H. Reddoch.** 1987. Notes on three Ottawa District orchids. Trail & Landscape 21: 18–26.

Reddoch, J. M., and **A. H. Reddoch.** 1997. The orchids in the Ottawa District: floristics, phytogeography, population studies and historical review. Canadian Field-Naturalist 111: 1–185.

Reddoch, J. M., and **A. H. Reddoch.** 2007a. Population ecology of *Platanthera hookeri* (Orchidaceae) in southwestern Quebec, Canada. Journal of the Torrey Botanical Society 134: 369–378.

Reddoch, J. M., and **A. H. Reddoch**. 2007b. Population Dynamics and Flowering Synchrony of *Goodyera pubescens* (Orchidaceae) in southwestern Quebec, Canada. Journal of the Torrey Botanical Society 134: 379–388.

Rowe, J. S. 1972. Forest Regions of Canada. Canadian Forestry Service, Department of the Environment. Ottawa, Ontario. 172 pages.

Sheviak, C. J. 1991. Morphological variation in the compilospecies *Spiranthes cernua* (L.) L.C. Rich.: ecologically-limited effects of gene flow. Lindleyana 6: 228–234.

Sheviak, C. J., and **P. M. Brown.** 2002. *Spiranthes casei*. Page 541 *in* Flora of North America north of Mexico. Volume 26. *Edited by* Flora of North America Editorial Committee. Oxford University Press, New York.

Sokal, R. R., and **F. J. Rohlf.** 1994. Biometry. The principles and practice of statistics in biological research. 3rd edition. Freeman and Co., New York. 859 pages.

Stoutamire, W. P. 1964. Seeds and seedlings of native orchids. Michigan Botanist 3: 107–119.

Tatarenko, I. V., and **K. Kondo**. 2003. Seasonal development of annual shoots in some terrestrial orchids from Russia and Japan. Plant Species Biology 18: 43–55.

Wells, T. C. E. 1967. Changes in a population of *Spiranthes spiralis* (L.) Chevall. at Knocking Hoe National Nature Reserve, Bedfordshire, 1962–65. Journal of Ecology 55: 83–99.

Wells, T. C. E. 1981. Population ecology of terrestrial orchids. Pages 281–295 *in* The biological aspects of rare plant conservation. *Edited by* H. Synge. Wiley & Sons, Toronto. 558 pages.

Wells, T. C. E., and **R. Cox.** 1989. Predicting the probability of the bee orchid (*Ophrys apifera*) flowering or remaining vegetative from the size and number of leaves. Pages 127–139 *in* Modern methods in orchid conservation: the role of physiology, ecology and management. *Edited by* H. W. Pritchard. Cambridge University Press, Cambridge. 183 pages.

Wells, T. C. E., and **R. Kretz.** 1983. *Spiranthes spiralis* (L.) Cheval. — from seed to flowering plant in 5 years. Watsonia 16: 235.

Willems, J. H. 1989. Population dynamics of *Spiranthes spiralis* in South-Limburg, The Netherlands. Mémoires de la Societé Royale de Botanique de Belgique 11: 115–121.

Willems, J. H. 2002. On the relation between vegetative and generative reproduction in *Spiranthes spiralis*. Eurorchis 14: 9–15.

Willems, J. H., and **E. Dorland.** 2000. Flowering frequency and plant performance and their relation to age in the perennial orchid *Spiranthes spiralis* (L.) Chevall. Plant Biology 2: 344–349.

Whiting, R. E., and **P. M. Catling.** 1986. Orchids of Ontario. CanaColl Foundation, Ottawa, Ontario. 169 pages.

Wilson, A. E. 1938. Ottawa sheet (31G/5, west half). Map 414A. Canada Department of Mines and Resources, Ottawa, Ontario. Map.

Received 26 November 2008
Accepted 30 May 2009